The Role of Poor Water Quality and Fish Kills in the Decline of Endangered Lost River and Shortnose Suckers in Upper Klamath Lake

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Abstract

*Lost River (*Deltistes luxatus*) and shortnose (*Chasmistes brevirostris*) suckers are federally endangered species endemic to shallow lakes of the Upper Klamath River Basin in Oregon and California. Upper Klamath Lake represents the majority of the remaining habitat of these suckers, but has been a site of intermittent fish kills. We studied fish kills and associated water quality dynamics in the lake in 1995, 1996, and 1997 to determine factors responsible for die-offs. Over 7,000 dead suckers were collected in the three years, and 85% of annual collections occurred during a 15-20 day period that began between mid August and late September. Suckers collected during the fish kills, as well as live fish captured the following spring, had a high incidence of afflictions such as parasitic and bacterial infections, cysts, and ulcers. The 1995 and 1996 fish kills were biased toward larger species (suckers), and larger individuals within species. Water quality in the lake was largely influenced by the dynamics of the blue-green algae* Aphanizomenon flos-aquae, *which comprised over 90% of algal biomass. Associated with each fish kill was an extended period of water column stability and high algal biomass (>150 µg L^{-1} chlorophyll* a*) before the kills, followed by a well-mixed water column and algal collapse with little residual algae. Before the kills, algal photosynthesis caused high pH (9-10) for 30-90 days, which maintained a large proportion of the total ammonia in the toxic, un-ionized form (200-2000 µg L^{-1} NH_3). Algal collapse decreased photosynthesis and increased biological oxygen demand, leading to dissolved oxygen levels less than 4.0 mg/l throughout the water column for 10-24 hours a day, for up to several days. Fish mortality coincided with algal bloom collapse and continued for 20-30 days after the period of low dissolved oxygen. We concluded that hypoxia, caused by the collapse of* A. flos-aquae *blooms, was the primary mechanism that triggered the 1995-97 fish kills. The susceptibility of fish to hypoxia was probably enhanced by chronic exposure to stressful levels of pH, ammonia, and dissolved oxygen during summer months prior to and during initiation of the kills. Exposure to water quality stressors also made fish susceptible to disease, which probably caused much of the post-hypoxic mortality. Dramatic decreases in the abundance of adult spawners after the fish kills indicate that poor water quality caused by the predominance of A. flos-aquae is a significant threat to the long-term persistence of the endangered suckers. Restoration efforts should focus on shifting the phytoplankton community toward a mixed-species assemblage as once existed, which would be less likely to develop extreme biomass levels and cause die-offs.*

Introduction

Habitat loss and degradation have contributed to worldwide native fish decline and extinction (Miller et al. 1989; Moyle & Leidy 1992; Williams & Neves 1992). Habitat degradation through eutrophication from agricultural non-point pollution has been designated as one of the leading threats to imperiled freshwater fauna in the United States (Richter et al. 1997). Increased eutrophication has lead to decreased water quality, which in turn has led to fish kills (Welch 1992; Carpenter et al. 1998). Hypereutrophic conditions and fish kills in Upper Klamath Lake, Oregon have involved federally listed endangered fishes, Lost River (*Deltistes luxatus*) and shortnose (*Chasmistes brevirostris*) suckers (USFWS 1988).

Lost River and shortnose suckers are endemic to shallow lakes of the Upper Klamath Basin, Oregon and California (Moyle 1976; Minckley et al. 1986). They are long-lived (30-40+ years) species that occupy lacustrine environments, except for spawning migrations up tributaries in late winter and spring (Scoppettone & Vinyard 1991). In the late 1800s and early 1900s, the suckers were abundant and supported subsistence and commercial fisheries (Cope 1879; Howe 1968), as well as a major sport and Native American subsistence fishery in the 1960s and 1970s (Coots 1965). However, censuses in the mid-1980s indicated that the numbers of adult suckers in Upper Klamath Lake were critically low and decreasing, which led to federal designation of both species as endangered (USFWS 1988). Both suckers are relegated to Upper Klamath Lake and a few smaller reservoirs and sumps in the basin.

Based on historical reports, Upper Klamath Lake has been eutrophic since at least the mid-1800s, but wetland drainage and agricultural development beginning in the late-1800s and accelerating through the 1900s is strongly implicated as the cause of its current hypereutrophic character (Bortleson & Fretwell 1993). Each summer the lake experiences extremely high pH, broad daily shifts in dissolved oxygen (anoxic to supersaturated), and high ammonia (Wood et al. 1996; Kann 1998; data presented herein). Summer fish kills of variable magnitude have been noted in Upper Klamath Lake since the late 1800s (Table 1), and usually involved large chubs (*Gila* sp.), adult suckers, or both. In recent years, fish kills have occurred more frequently, with substantial die-offs each year from 1995-1997. Examination of suckers from the recent die-offs indicated

Table 1. Reported fish kills (or indications thereof) in Upper Klamath Lake, 1894 to 1994. See text for description of fish kills from 1995 to 1997.

Date	Fish observed*	Location	Symptoms/Causal agents	Source
1894 mid June	mostly LR, SN, and KL, but also large TC	the lake and the Link River	missing portions of fins; disease that destroyed the eyes and turned skin around the head yellow	Gilbert (1898)
1928 summer	mostly fish > 30 cm (probably chubs or suckers)	shore near Modoc Point	not specified	Wil Dean (Klamath resident)
1932 summer	hundreds of suckers	shore near Modoc Point	not specified	D. Mote, Oregon State College
1960's	millions of chubs	not specified	bacterial disease	Howe (1979)
1967 and 1968	thousands of LR	LR moved from the lake up to the base of the Sprague R. dam	poor water quality?	Golden (1969)
1971 summer	14 million fish; mostly large TC, but also some large LR and BC	not specified	columnaris disease *Lernaea* infestation	Rohovec and Fryer (1979)
1986 late August	~ 200 LR and 10 SN collected; chub observed	suckers and chub at mouth of Pelican Bay; chub also in the lake and the lower Williamson R.	hypoxia columnaris disease	Buettner and Scoppettone (1990)
1994 August and September	several LR, dozens of BC, and several RBT collected; additional chub observed	Pelican, Ball, and Shoalwater bays; main body of the lake.	hypoxia	Klamath Tribes, Bureau of Reclamation

*Species abbreviations: blue chub (BC), Klamath largescale sucker (KL), Lost River sucker (LR), rainbow trout (RBT), shortnose sucker (SN), and tui chub (TC).

that some had succumbed to disease; however, disease in fishes is frequently an artifact of stressful conditions (Wedemeyer & Mcleay 1981; Herman 1990). In this study we investigated the recent fish kills and associated water quality conditions to identify factors responsible for the die-offs, and the continued endangerment of Lost River and shortnose suckers.

Methods

Study Area

Upper Klamath Lake in south-central Oregon is one of the largest freshwater lakes in the western U.S. (~270 km^2 at full capacity; Fig. 1). Mean depth of the lake in mid summer is less than 2 m, and almost all deeper water (3-12 m) is restricted to narrow trenches along the western shore. Upper Klamath Lake's primary sources are the Williamson River (50%), Wood River (16%), and subsurface and spring flow (14%; Hubbard 1970). Since 1921, the lake's outflow has been controlled at Link River Dam, which allows water level to drop 1.2 m below pre-dam minimum, and the relinquishment of more than 50% of the historic water volume. Much of the water released from the lake is either diverted for irrigation or is passed through hydroelectric facilities before reaching the Link River, and then the Klamath River. In addition to hydrologic changes associated with dam operation, the watershed has been greatly altered through forest clear-cutting, cattle grazing, and the conversion of wetlands to pasture and agriculture (Bortleson & Fretwell 1993; Kann 1998).

Fish Kill Assessment

Fish kills were sampled upon their initial detection to at least three weeks after the majority of fish had died. Effort invested in collection of dead fish was commensurate with the magnitude and duration of each kill; peak collection closely matched peak availability of intact carcasses. Sites throughout the lake were surveyed to assess the spatial extent of the fish kills; however, much of the effort was directed at areas where moribund and dead fish were concentrated, such as shorelines and spring areas. High turbidity in the main body of the lake prevented observation of fish that might have been on the lake bottom; thus, fish were found either floating on the lake surface or washed onto shore. In spring areas, where water was clear, fish generally were found on the bottom and collected with dip-nets, although some floating fish were also collected. Collection efforts were focused on dead suckers. When possible, fish were identified as to

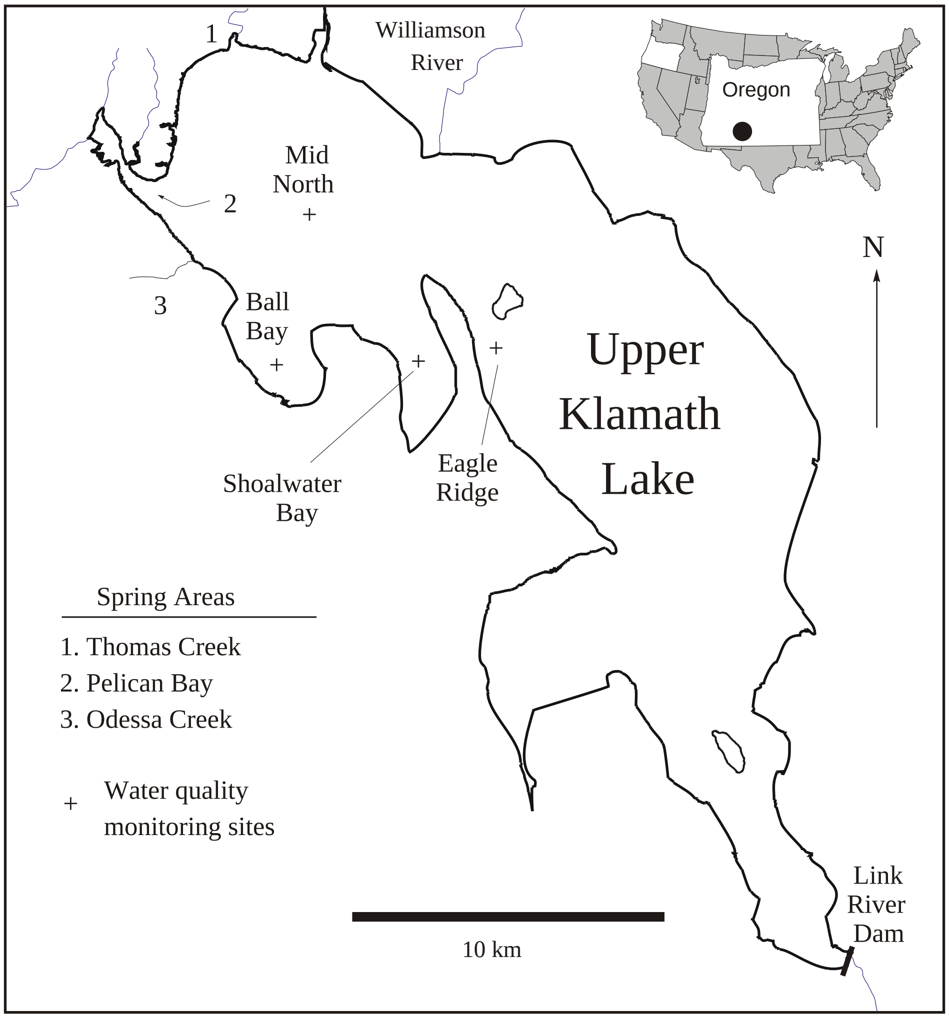


Figure 1. Map of Upper Klamath Lake, Oregon.

species and their fork length (FL) measured. The size distribution of suckers collected from the fish kills were compared with conspecifics captured in spring stock assessments of the same year (Perkins et al. 2000).

Water Quality Dynamics

Water quality data used to assess the relationship between water quality and fish kill dynamics were derived from data sets collected by the Klamath Tribes and the U.S. Bureau of Reclamation. The first set characterized water quality throughout the water column at a given point in time (hereafter called "profile data"). The second set consisted of measurements recorded hourly at a depth of 1 m (referred to here as "hourly data").

Profile Data

Profile data consisted of limnological measurements made in Upper Klamath Lake by the Klamath Tribes from 1990 through 1997 to monitor seasonal water quality and the dynamics of nutrients, phytoplankton, and zooplankton (see Kann 1998 for complete details). Because our intent was to focus on water quality associated with fish kills, rather than to provide a detailed description of annual water quality and limnological dynamics, we analyzed only a subset of the profile data. This subset consisted of biweekly (and weekly in 1990) measurements from June through October at three sites: Eagle Ridge (ER), Mid North (MN), and Shoalwater Bay (SB) (Fig. 1). We focused on these northern sites because adult suckers tend to occupy this part of the lake in summer (M. Buettner, U.S. Bureau of Reclamation, personal communication), and because these sites provided the most consistent data set for interannual comparisons.

Depth profiles of temperature, pH, and dissolved oxygen (DO) were measured with a Hydrolab Surveyor® multi-parameter probe that had been calibrated immediately prior to usage. Data were typically collected between 1200 and 1500 hours. Measurements were taken at 1-m intervals starting at the surface, with an off-bottom reading taken at 30 cm above the bottom. Water column means were computed based on depth-weighted values (e.g., surface and off-bottom values were weighted less than mid-column values). Algal biomass (as indicated by Chlorophyll *a*), and ammonia nitrogen (NH_4-N) were measured from depth-integrated samples of the water column that were taken concurrently with the water quality profiles. The un-ionized fraction of ammonia (NH_3-N) was computed based on the water-column mean pH and temperature (Emerson et al. 1975).

Linear regression (Wilkinson 1999) was used to determine the relationship between net change in algal biomass (chlorophyll *a*; mean of July-August) and minimum water column dissolved oxygen (mean of July-August) computed from bi-weekly profile data from 1990-1997. Mean net change in algal biomass for the July-August period was computed as:

$$\frac{(B_{t2} - B_{t1}) + (B_{t3} - B_{t2}) + \cdots (B_{tn} - B_{tn-1})}{n}, \quad t = 1, \ldots, n$$

where *B* is the biomass at sample date *t*, and *n* is the number of sample dates within the July-August period.

To compare water column stability, within and among years, we computed the relative thermal resistance to mixing (RTRM), which is an index of water column stability based on gradients in water density (Jones and Welch 1990). Weak density gradients result in low RTRM values and indicate little resistance to wind-induced mixing; high RTRM values indicate high resistance to mixing. For practical purposes, RTRM can also be viewed as an index of stratification. Linear regression (Wilkinson 1999) was used to determine the relationship between RTRM (mean of July-August) and the DO difference between surface and bottom (mean of July-August) computed from bi-weekly profile data, 1990-1997.

Hourly Data

Hourly data consisted of pH, dissolved oxygen, and temperature measurements recorded by Hydrolab DataSondes® deployed by the Bureau of Reclamation-Klamath Project Office at a depth of 1 m at three sites in the northern area of the lake. Two of these sites coincided with the profile data described above (MN and SB), and the third was located in Ball Bay (Fig. 1). Recorders were deployed for approximately one-week intervals, and then replaced with a newly calibrated recorder. Our analyses focused on data collected from June through early-October, 1995-1997, which were the years with large die-offs of adult suckers. Days with less than 20 hourly measurements were excluded from analyses. Hourly data were subject to rigorous quality assurance that included verification of recorder accuracy through pre- and post-deployment calibrations, and by comparing recorder data from deployment and retrieval dates with measurements from a second, independently calibrated recorder (M. Berg, U.S. Bureau of Reclamation, personal communication).

Results

Fish Kills

In 1995 and 1996, adult Lost River and shortnose suckers dominated the die-offs, with blue chub (*Gila coerulea*) and tui chub (*G. bicolor*) comprising less than 5% of dead fish observed. In the 1997 die-off, suckers were numerous (Table 1) but far outnumbered by chubs, tens of thousands of which were seen scattered across the lake. Only a small fraction of dead suckers observed were collected because of their widespread distribution. Of the suckers collected, many (37-71%) were from spring areas where high densities and clear water enhanced collection efficiency (Fig. 2). The ratio of Lost River suckers to shortnose suckers was consistently higher in collections from the lake than collections from the spring areas. Lost River suckers were more numerous than shortnose suckers in 1995 and 1996, but less numerous in 1997 (Fig. 2). Other species observed in the 1995-1997 die-offs included the endemic marbled sculpin (*Cottus klamathensis*), Klamath largescale sucker (*Catostomus snyderi*; not observed in 1995), and redband trout (*Oncorhynchus mykiss)*. Brown bullhead (*Ictalurus nebulosus*) were observed only in 1997. Redband trout were more prevalent in 1997 than other years (90 trout were collected in 1997 as compared to three in 1996 and none in 1995). Most fish collected during the fish kills in 1996 and 1997 had one or more physical afflictions, particularly infestations of *Lernaea* sp. and other parasites. Gill lesions indicative of columnaris disease were observed in some fish, but not others. Fish afflictions were not routinely recorded in 1995.

Among the three study years, 1995 had the least severe fish kill with only 472 dead suckers collected. The 1995 kill occurred later than 1996 and 1997, with 84% of suckers collected during the last 19 days of September and a peak on 23 September (Fig. 2). In 1996, dead suckers were found over a broad time period (16 July to 3 October), but 93% of 4453 were collected from 26 August to 12 September (18 days) and peak collection was on 3 September (Fig. 2). In 1997, dead suckers were collected from 23 July to 22 September, with 86% of 2335 collected

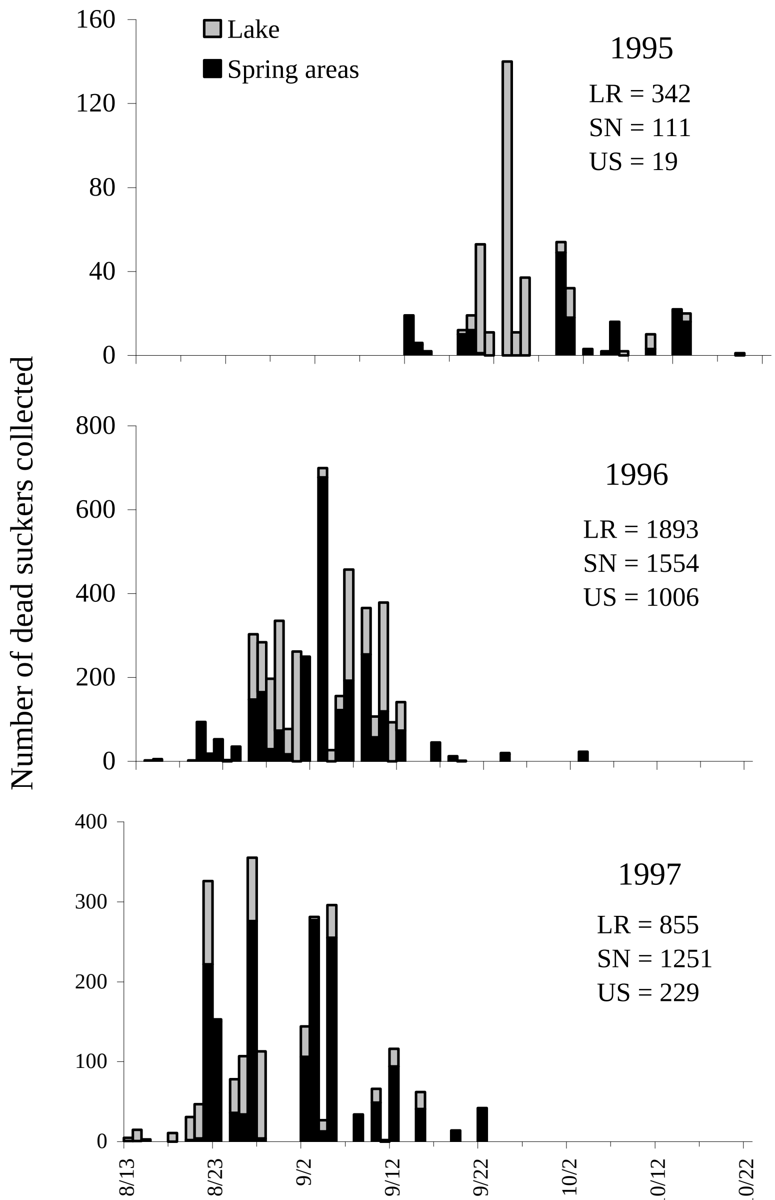


Figure 2. Daily number of suckers collected during fish kills in Upper Klamath Lake, 1995-1997.

during the 20 days from 20 August to 8 September with several peaks in collections in this period (Fig. 2).

In each of the three kills, the majority of suckers were adult-sized; most shortnose suckers were > 330 mm FL and most Lost River suckers were > 400 mm FL (Figs. 3 and 4). Cohorts of smaller shortnose suckers (290-330 mm) and Lost River suckers (320-400 mm) were observed in 1997 (Fig. 4). These cohorts were virtually absent from the 1995 fish kill, and in the 1996 fish kill, only the cohort of Lost River suckers was present in appreciable numbers.

The daily mean length of suckers collected from the fish kills was fairly constant over time in some instances (e.g., shortnose suckers from the spring areas in 1997), but highly variable in other instances (e.g., shortnose suckers from the spring areas in 1996; Fig. 3). In some cases, the daily mean lengths of Lost River and shortnose suckers followed the same trends over time (e.g., spring areas in 1996; Fig. 3). The modal size of shortnose suckers in the die-offs was consistently 10-30 mm larger than fish captured during the stock assessment of the previous spring (Fig. 4). This was in contrast to observations that shortnose and Lost River suckers tagged in the stock assessment showed little increase in length when recaptured in the die-off of the same year. The change in length ranged from -16 to 10 mm for 15 recaptured shortnose suckers and -22 to 1 mm for five recaptured Lost River suckers.

Water Quality and Algal Dynamics[1]

Algal Biomass

Substantial algal biomass (>150 μg L^{-1} chlorophyll *a*) occurred each year from 1995 to 1997 (Fig. 5) and was comprised almost entirely of the blue-green alga *Aphanizomenon flos-aquae* (>90% by weight). A large algal decline preceded each fish kill in 1995-1997 (Fig. 5). In 1995, the kill began during a 2-week chlorophyll *a* decline of 129 μg L^{-1}; in 1996 and 1997, the kills occurred after 4-week declines of 137 μg L^{-1} and 217 μg L^{-1}, respectively. The September 1995 biomass decline preceded the 1995 fish kill, and was the year's second such decline. The first decline occurred during a 2-week period in August and was not followed by a fish kill, but the biomass decline was less than September (96 μg L^{-1} vs. 129 μg L^{-1} chlorophyll *a*) and the algal

[1] Values reported are the mean of the three sites noted in the Methods unless indicated otherwise

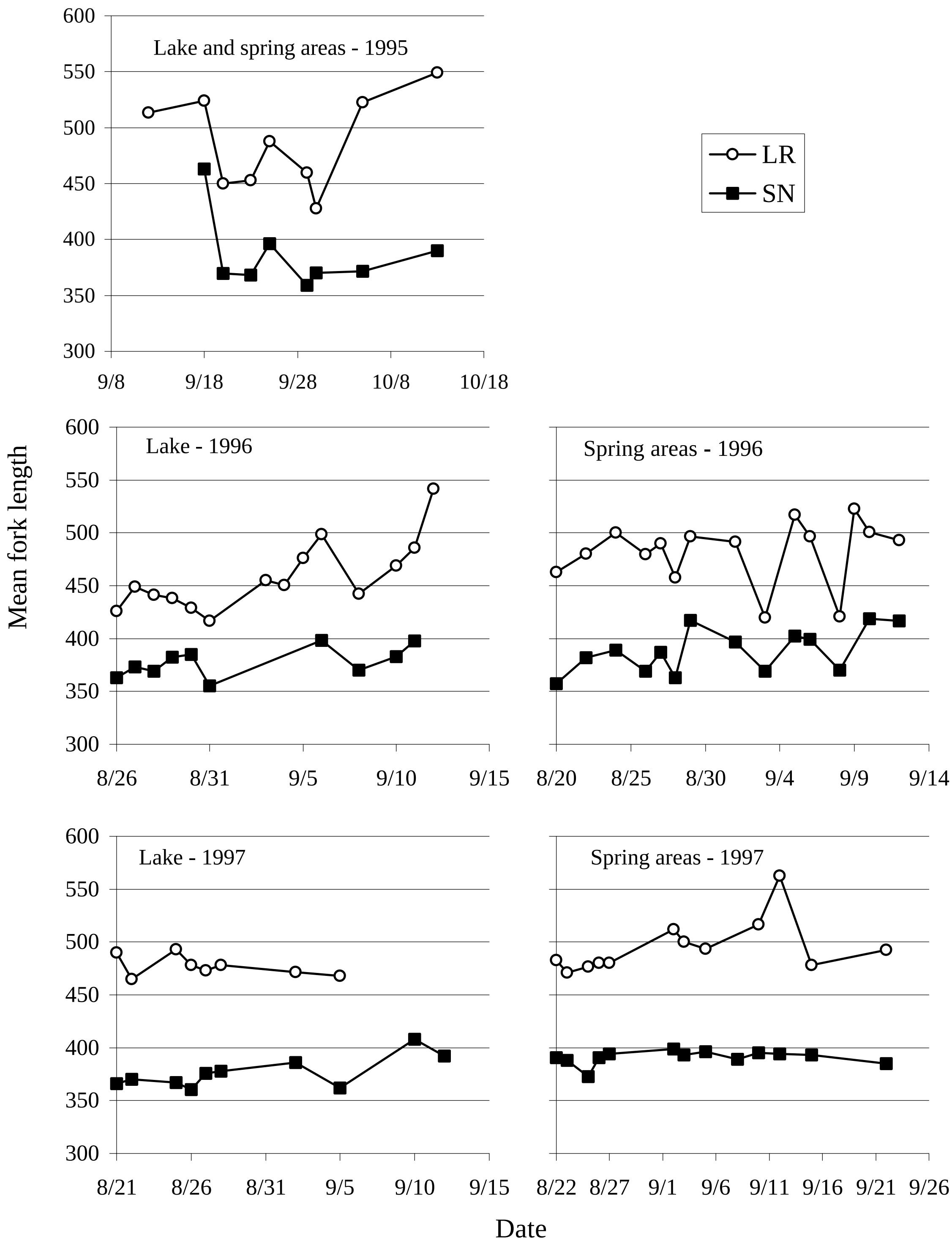


Figure 3. Daily mean fork lengths of Lost River (LR) and shortnose suckers (SN) collected in from fish kills in Upper Klamath Lake, 1995-1997. In 1995, data from spring areas and the main lake were not separated because of small sample sizes.

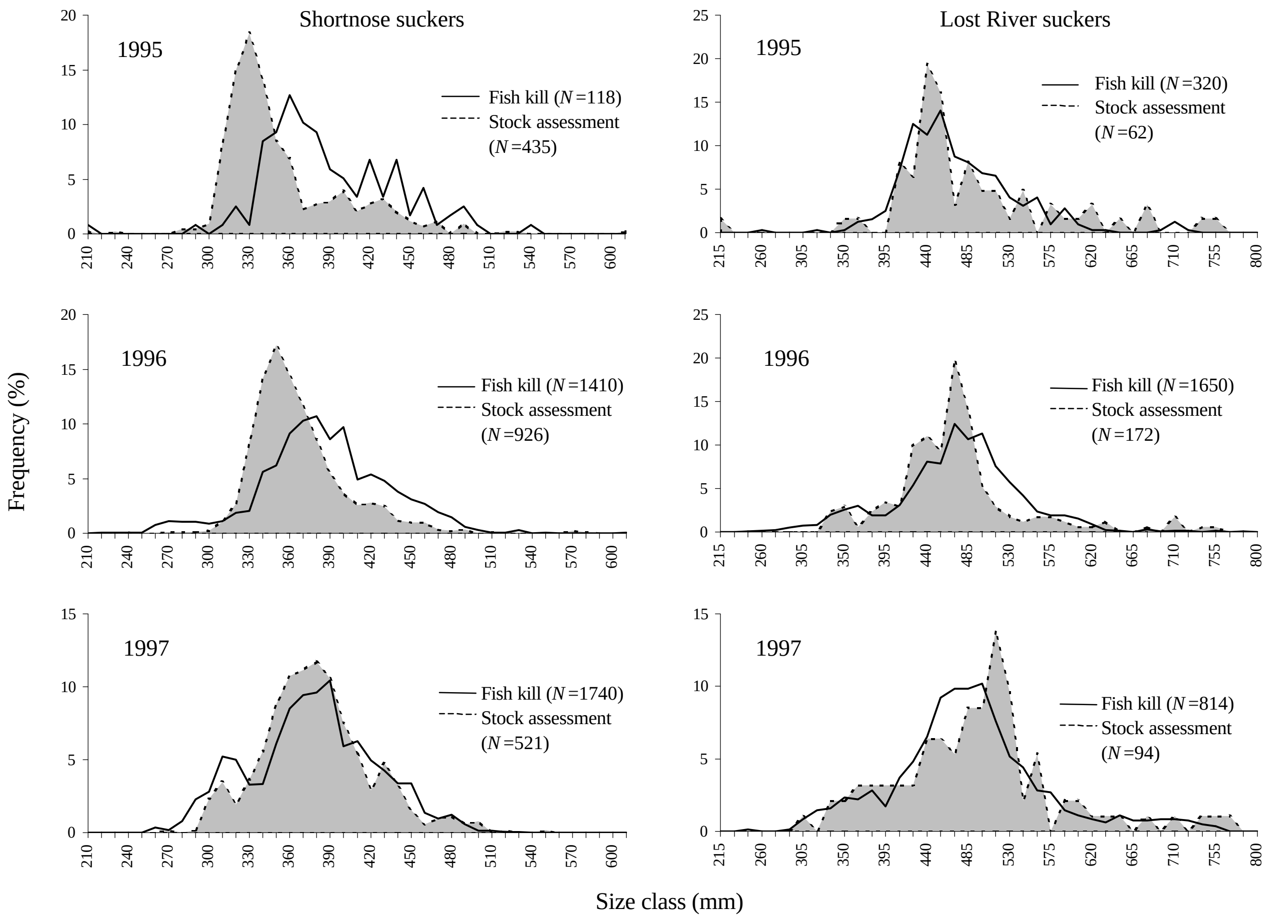


Figure 4. Comparison of length frequencies between suckers collected during the fish kills in Upper Klamath Lake, 1995-1997, and conspecifics captured in stock assessments in spring of the same year.

biomass that remained after the August decline was 26% greater than after the September decline (82 µg L^{-1} vs. 65 µg L^{-1} chlorophyll *a*). Differences between the first and second algal declines in 1995 were even more substantial when the Mid North site was examined separately. At this site, chlorophyll *a* decreased 113 µg L^{-1} during the first decline (108 µg L^{-1} remaining), and 197 µg L^{-1} during the second decline (16 µg L^{-1} remaining). Profile data from 1990-1997 showed a significant positive relationship (r^2=0.95; P<0.0001) between net change in algal biomass (mean of July and August) and minimum DO (mean of July and August; Fig. 6).

Temperature

From 1995 to 1997, mean daily water temperature at 1 m depth reached 20°C in early July, and remained between 20 and 25 °C for most of July and much of August, with an annual peak in late July or early August (Fig. 5). Among the three sample sites, maximum daily water temperature greater than 27 °C was recorded only six days, five of which were in 1996. The 1995-1997 fish kills began 14-36 days after the annual peak water temperature. Mean daily water temperatures were 16-22°C during the kills (Fig. 5).

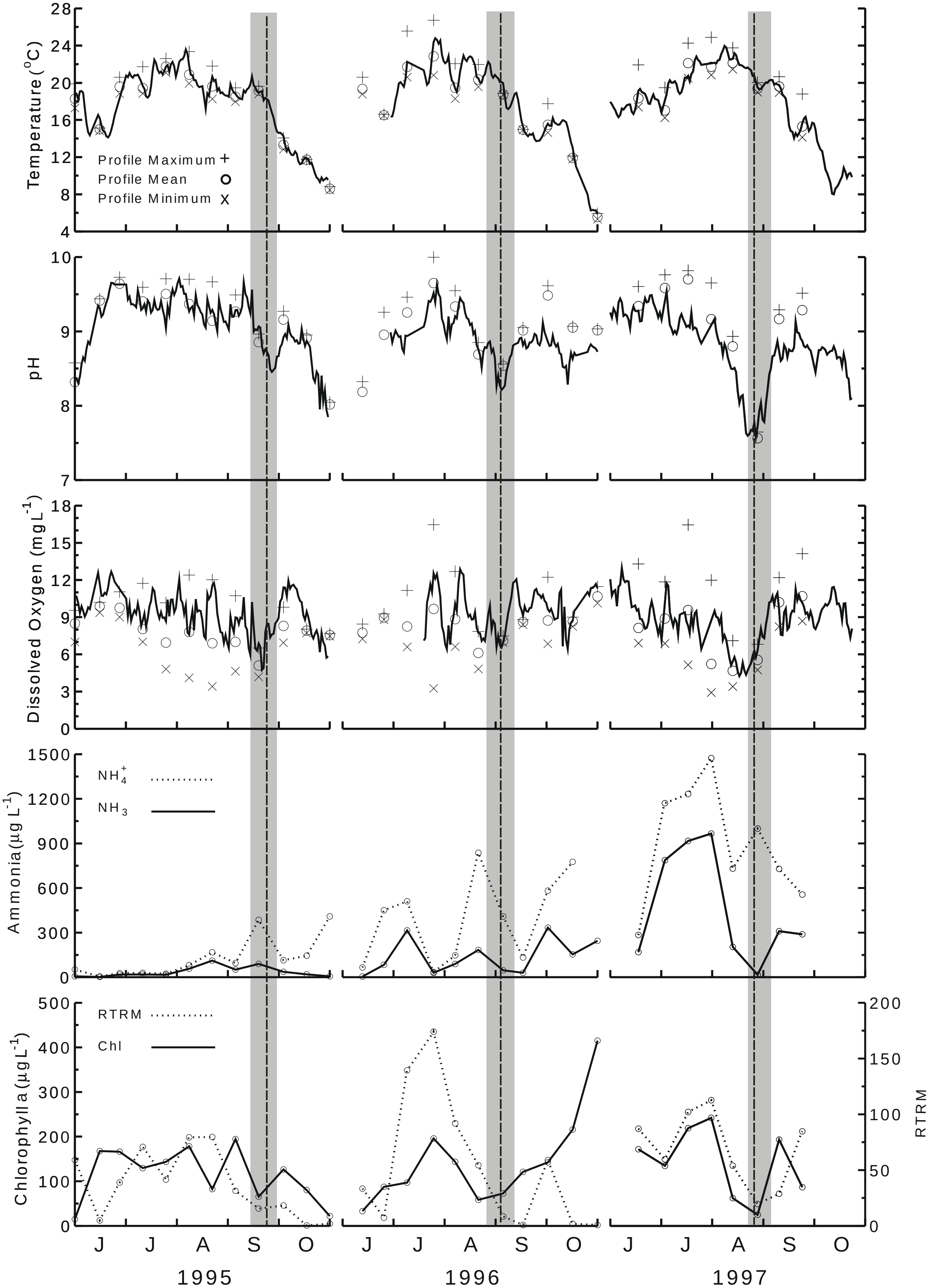
Ammonia

In 1995, un-ionized ammonia (NH_3) was generally below 200 µg L^{-1} at Mid North and Shoalwater Bay, but was 200-300 µg L^{-1} at Eagle Ridge for parts of July, August, and September (Fig. 7). In 1996, high levels of un-ionized ammonia were observed at all three sites in July (200-400 µg L^{-1}) and October (200-900 µg L^{-1}). In 1997, the magnitude, duration, and spatial extent of elevated un-ionized ammonia were substantially greater than the previous two years, with un-ionized ammonia commonly at 500-2000 µg L^{-1}. An extended period of high ammonia preceded the fish kill in 1997, and to a lesser extent the other years; but, during the peak of each fish kill, un-ionized ammonia was consistently <100 µg L^{-1} (Fig. 5). The declines in ammonia that occurred prior to fish kill peaks coincided with decreasing water column stability, algal biomass, and pH (Fig. 5).

pH

Mean daily pH at 1 m depth was 9.0-9.6 for one to three months each summer (from mid June through mid September in 1995, from mid July through mid August in 1996, and for all of June

Figure 5. Water quality conditions occurring during Upper Klamath Lake fish kill years, 1995-1997. Vertical dashed lines represent the peak in collection of dead fish for each year, and vertical shaded areas represent the period in which 85% of dead fish were collected. Hourly data measured at 1 m for temperature, pH, and dissolved oxygen (solid lines) represent the daily mean of three sites: Ball Bay, Shoalwater Bay, and Mid North. Profile data for these same parameters, as well as for ammonia, chlorophyll *a*, and water column stability (RTRM) represent the mean of data collected bi-weekly at Ball Bay, Shoalwater Bay, and Eagle Ridge.


Temperature (°C)
Profile Maximum +
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Profile Minimum X
pH
Dissolved Oxygen (mg L-1)
Ammonia (µg L-1)
NH4+
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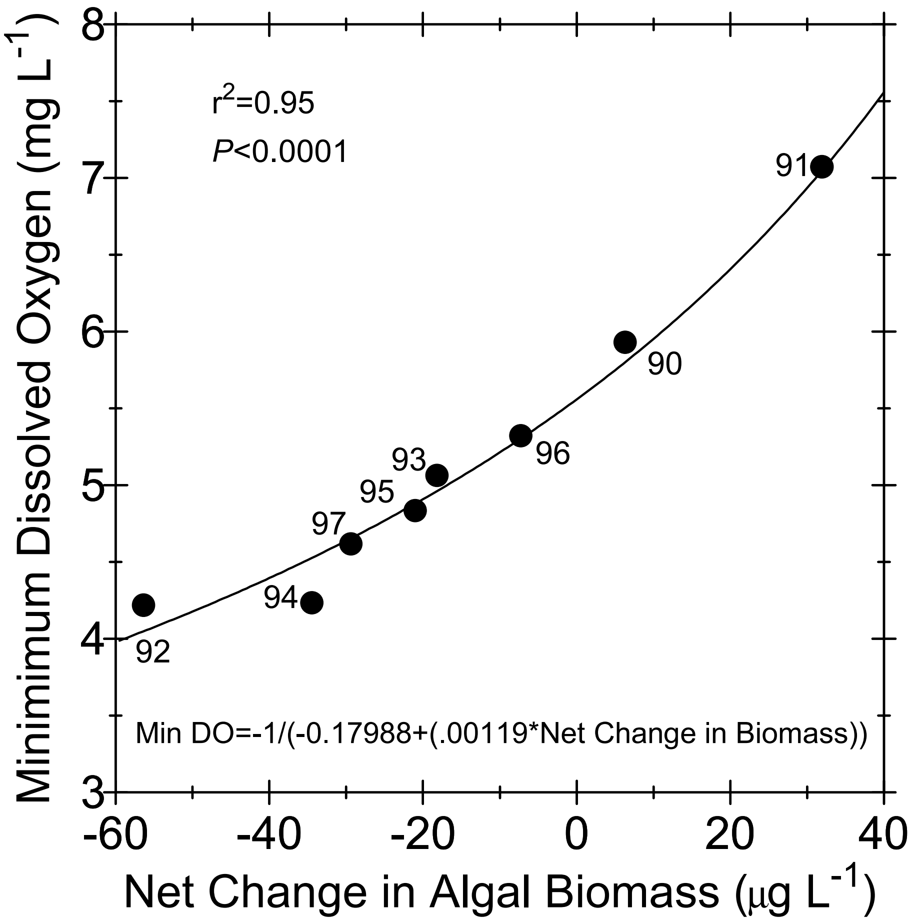

Figure 6. Relationship between net change in algal biomass (chlorophyll *a*; mean of July-August) and minimum water column dissolved oxygen (mean of July-August) computed from bi-weekly profile data in Upper Klamath Lake, 1990-1997.

and July in 1997) (Fig. 5). During the above periods, daily maximum pH at 1 m depth averaged 0.26 units higher than the daily mean, and rarely exceeded 10. Mean pH declined below 9.0 in late summer each year, and corresponded to declines in algal biomass. During the fish kills, pH was less than 9.0, except for the early part of the 1995 kill. The peak of the fish kills occurred when pH was at some of the lowest values (7.5-8.5) of summer and early fall (Fig. 5).

Dissolved Oxygen

Mean daily DO at 1 m depth fluctuated widely (4-13 mg L^{-1}) during summer months, 1995-1997 (Fig. 5). Profile data showed that instances of mean off-bottom DO <4 mg L-^{1} occurred prior to fish kills each year. Each fish kill coincided with a period of decreased mean daily DO (Fig. 5) and was associated with increased occurrence of hourly DO values less than 4 mg L^{-1} (Fig. 8). Near the onset of the fish kills, DO was typically less than 4 mg L^{-1} for 10-24 hours per day (at 1 m depth), for several days, at one or more sites (Fig. 8). In most instances, this included shorter periods when DO was 0-2 mg L^{-1}. The spatial extent, duration and magnitude of hypoxia was greatest in 1997, which was the only year that DO <4 mg L^{-1} was observed at Mid North (Fig. 8).

Oxygen saturation (mean daily at 1m depth) generally exceeded 100% during periods of active algal growth, and daily maximums commonly exceeded 175% saturation. However, during periods of algal decline and fish kills, saturation at 1m tended to be less than 100% during the day, and less than 20% during the night. Near the bottom, saturation tended to be less than 20% during day and night during fish kills (profile data).

Water Column Stability

Each fish kill was preceded by relatively high water column stability (RTRM>50) for four to eight weeks, followed by a decline in RTRM to low levels (<25) at the peak of the kills (Fig. 5). In 1996 and 1997, the period of highest stability corresponded to the highest water temperatures. Mean RTRM (July-August) was higher in the years with large fish kills (1995-1997) than the preceding five years (Fig. 9), and a significant positive relationship existed between RTRM and the difference between the surface and off-bottom dissolved oxygen levels (r^2=0.95, P<0.001; Fig. 9).

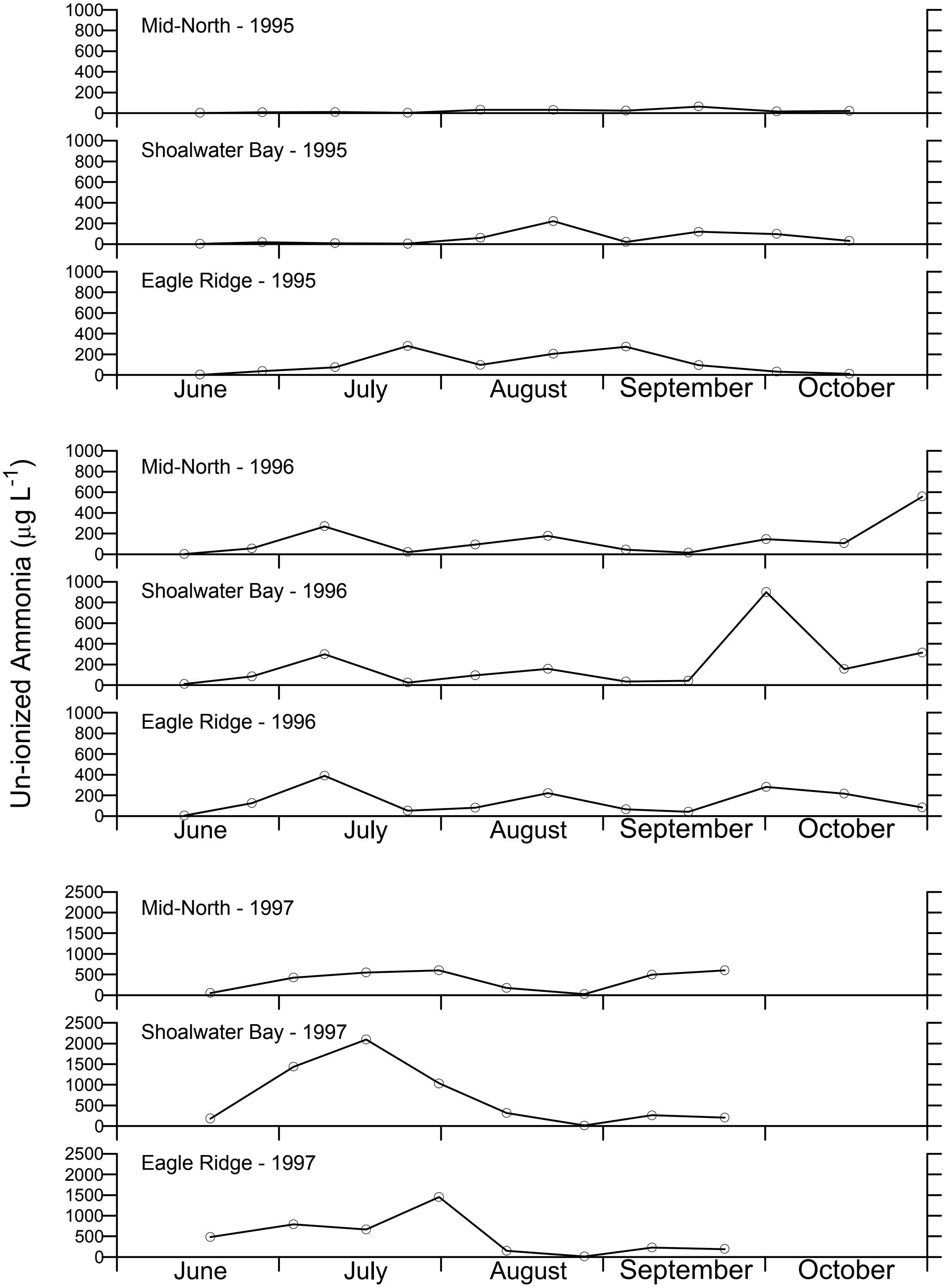

Figure 7. Bi-weekly un-ionized ammonia concentration at three northern sites (Ball Bay, Shoalwater Bay, and Eagle Ridge) during Upper Klamath Lake fish kill years, 1995-1997

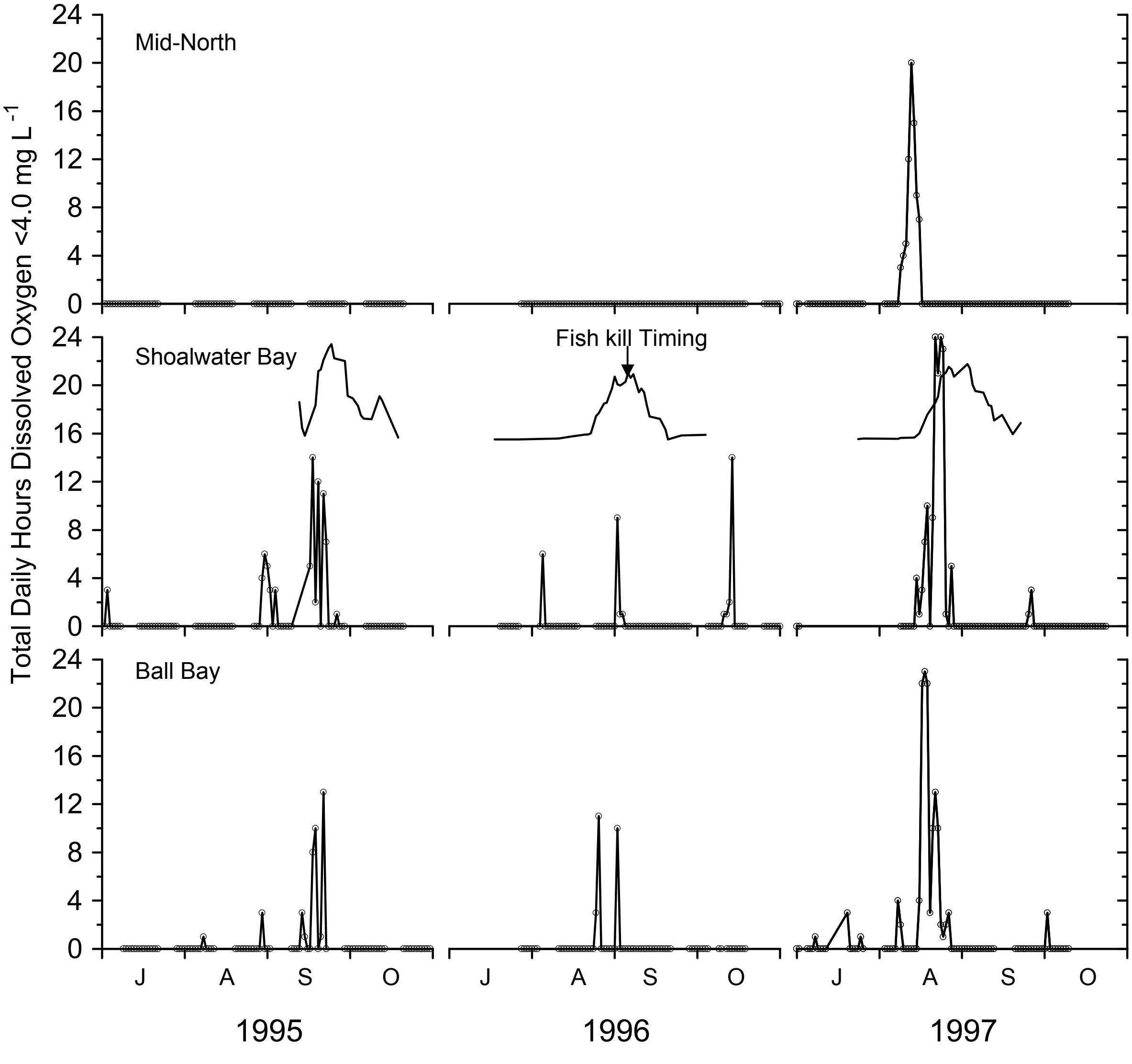

Figure 8. Daily number of hours that dissolved oxygen was less than 4 mg L^{-1} (solid lines with symbols) computed from hourly data measured at 1 m at three sites (Ball Bay, Shoalwater Bay, and Mid North) during Upper Klamath Lake fish kill years, 1995-1997. Solid lines (no symbols) in the middle panel represent the dead fish collected each year, expressed as a 2-day running mean of the daily percent of total dead fish collected within a year.

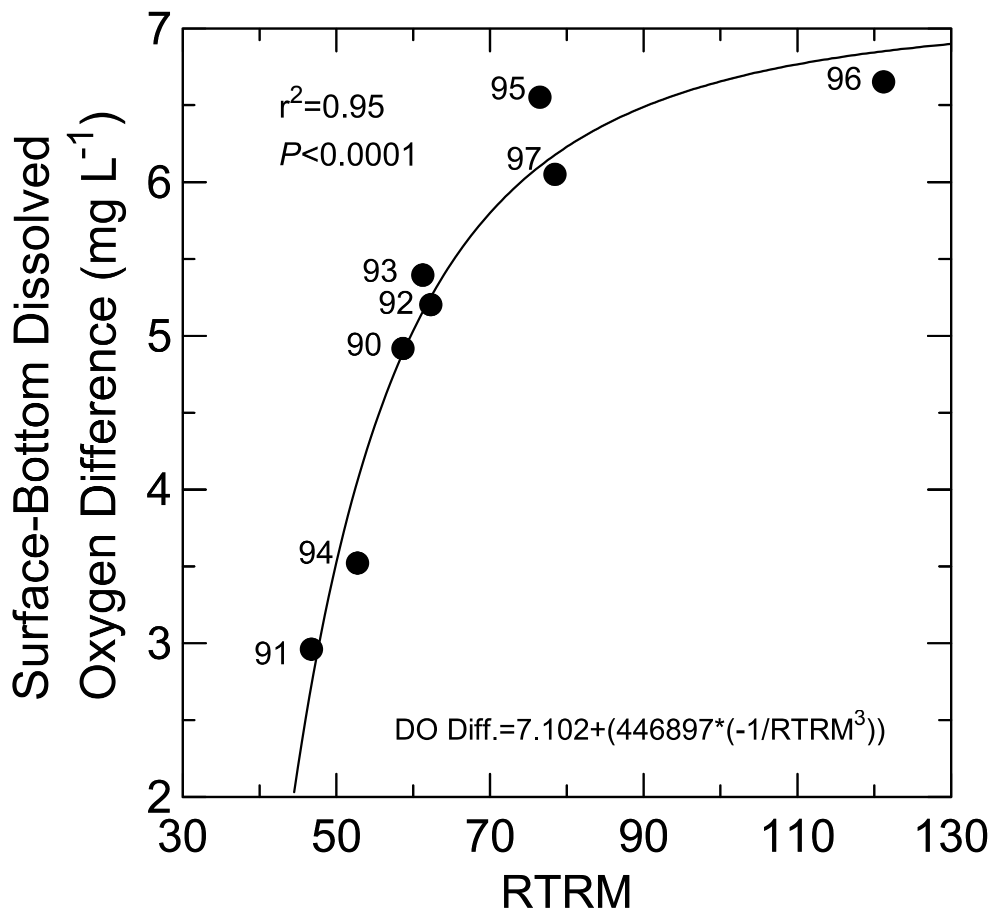

Figure 9. Relationship between water column stability (RTRM; mean of July-August) and the dissolved oxygen difference between lake surface and bottom (DO Diff.; mean of July-August) computed from bi-weekly profile data in Upper Klamath Lake, 1990-1997.

Discussion

Fish kills result from a variety of natural and artificial factors (Meyer and Herman 1990). Determination of the cause of fish kills is an investigative process that often must rely on circumstantial evidence; however, given sufficient information about a fish kill and the associated environmental conditions, the cause can usually be determined with an acceptable level of certainty. Below we discuss the information associated with the 1995-1997 fish kills in Upper Klamath Lake, and consider three mechanisms that have received attention as possible contributors to the fish kills: poor water quality, algal toxins, and disease.

Size and Species Composition of Fish Killed

The size and species composition of fish killed during a die-off is often indicative of the die-off cause (Trim and Marcus 1990). For example, in die-offs caused by toxic compounds, small fish usually die before larger conspecifics (Wedemeyer et al. 1976; Meyer & Herman 1990) presumably due to higher metabolic rate and faster accumulation of toxins relative to biomass. Conversely, in die-offs caused by hypoxia, larger fish often die before, and sometimes in the absence of smaller fish (Casselman & Harvey 1975; Hunn & Schnick 1990; Meyer & Herman 1990). Presumably, large fish are more readily affected by low DO, even though metabolic rate drops with increased fish size, because gill surface area to body mass decreases with increased fish size (C. Wood, McMaster University, personal communication). Field observations of larger fish being more susceptible to hypoxia contradicts some laboratory studies (e.g., Keys 1931; Moore 1942; Shepard 1955); however, the laboratory studies were restricted to a narrow size range of small (<180 mm) fish, which may account for the contradiction.

Four lines of evidence indicated large fish were most susceptible in the 1995 and 1996 Upper Klamath Lake fish kills, and thus implicated hypoxia as a mechanism causing death. First the fish kills were biased toward larger species (Lost River and shortnose suckers), and larger individuals within species. Second, Lost River suckers (the largest sucker in the lake) were more abundant than shortnose suckers in the 1995 and 1996 fish kills, despite spring stock assessments that indicated shortnose sucker were more abundant in the lake (Perkins et al. 2000). Third, the trends in the size of fish collected throughout the die-offs was remarkably similar between Lost River and shortnose suckers, which would not be expected if the fish kills had been random with respect to fish length (Fig. 3). Finally, the size distributions of shortnose suckers in the 1995 and 1996 die-offs were shifted about 30 mm larger than fish captured in the stock assessment of the previous spring (Fig. 4), and this shift was not attributable to growth (based on fish tagged in the stock assessment and recaptured in the fish kill).

The die-off in 1997 appeared less species and size selective than in 1995 and 1996. The relative abundance of chubs vs. suckers, and Lost River vs. shortnose suckers in the 1997 fish kill was consistent with that known to exist in the lake; i.e., chubs were much more abundant than suckers, and shortnose suckers were more abundant than Lost River suckers. Cohorts of juvenile Lost River and shortnose suckers that were known to exist in the lake were present in the 1997 die-off, unlike fish kills in the previous years. The daily mean length of dead suckers fluctuated less than in previous years (i.e., less size-selective variation; Fig. 3). Lastly, the difference in the size distribution of adult shortnose suckers from the fish kill and the stock assessment of the same year was less in 1997 than in 1995 and 1996 (Fig. 4).

Water Quality and Algal Dynamics

A similar pattern of water-column and algal dynamics was associated with each of the three fish kills studied. This pattern consisted of an extended period of water column stability and high algal biomass before the kills, followed by a well-mixed water column and algal collapse with little residual algae. Extended periods of water-column stability have been linked with proliferation of blue-green algae (Reynolds & Walsby 1975) and were observed during July and August in fish kill years 1995-1997, unlike 1990-1994 when few if any dead fish were observed (Fig. 9). The water column mixing that followed may have contributed to the algal bloom collapses by moving algae into deeper water with reduced light, which has been reported as the cause of algal bloom collapses (e.g., Barica 1977; Mericas & Malone 1984), rather than hot calm periods as previously accepted (Bennett 1971). Climatic factors that have caused mixing followed by bloom collapses, hypoxia, and fish kills, include a sharp drop in air temperature, strong wind, and rain (Swingle 1968; Barica 1978).

After bloom collapses, water-column DO, and consequently fish kill probability, are strongly influenced by the balance between increased biological oxygen demand and oxygen production by residual algae (Swingle 1968). Barica (1975b; 1978) found that kills only occurred when chlorophyll *a* exceeded 100 µg L^{-1} and declined by more than 70 µg L^{-1} per week, and that the severity of kills after *A. flos-aquae* collapse was proportional to peak algal biomass. Observations from Upper Klamath Lake were consistent with Barica's studies; chlorophyll *a* exceeded 200 µg L^{-1} each summer, 1995-1997, and the kills were preceded by declines of 129-217 µg L^{-1}, with residual levels less than 70 µg L^{-1} (Fig. 5). Further evidence of the strong influence of algal bloom dynamics on DO concentration is shown by the significant positive relationship between net change in algal biomass and minimum DO during July-August (Fig. 6). A mixed water column, as observed during the 1995-1997 fish kills, also means that oxygen production by residual algae is hindered due to reduced time in the photic zone, and fish cannot avoid low DO, as they can when low DO is restricted to bottom waters, as occurred prior to the kills.

Several observations indicated that water quality conditions in Upper Klamath Lake were stressful to fish near the time of the die-offs. First, atypical fish movement out of the main body of the lake occurred just prior to, and during, the fish kills. This included movement of thousands of suckers to spring areas, and increased movement of fish into irrigation canals. Second, shortly before the die-off in 1997, we observed that captured suckers held in the lake surface water exhibited disequilibria within 15 minutes. Third, in the summer of 1995, hatchery-reared Lost River suckers held in cages died within 24-48 hours at two of eight lake sites; the deaths were attributed to hypoxia (Martin 1997). These behavioral and physiological indications of a stressful environment are not unexpected given the water quality conditions, which are discussed below.

Temperature

From 1995-1997, the daily maximum water temperature in Upper Klamath Lake rarely exceeded 26^{o}C, which is within the "preferred" and "optimum" temperature range of many warmwater species (see reviews by Coutant 1977; Alabaster & Lloyd 1980; Elliot 1981). Thermal tolerance studies of adult suckers from Upper Klamath Lake have not been conducted, but Castleberry and Cech (1993) determined that the thermal maxim of age 0+ shortnose suckers was 32.1-33.3^{o}C, and Saiki et al. (1999) calculated a mean 96-hr LC_{50} value of 30.5 ^{o}C for Lost River and 30.4 ^{o}C for shortnose suckers (3-7 month old juveniles). During the fish kills, mean daily water temperature was 16-20 °C (Fig. 5), which is substantially less than stressful levels mentioned above.

pH

In the summer months before the fish kills, the pH in Upper Klamath Lake was frequently in the range (9-10) that has been shown to have negative effects on fish (Kann 1999); however, during the greater part of the die-offs, pH was at less stressful levels. Studies have shown that elevated environmental pH (9-10) can have lethal and sublethal effects such as impaired ammonia excretion and sodium influx (Wright & Wood 1985), elevated blood ammonia levels (Randall & Wright 1989), edema of gills (McKenna & Duerr 1976), and hypertrophy of gill mucous cells (Daye & Garside 1976). Rainbow trout (*O. mykiss*) exposed to alkaline water had reduced swimming ability (Ye & Randall 1991) that may have been due to acid-base disturbances and associated effects on oxygen transport, ionic and osmotic changes and/or ammonia accumulation in body tissues (Randall & Brauner 1991). Falter and Cech (1991) found that small (1-3 g) tui chubs, Klamath largescale suckers, and shortnose suckers from the Upper Klamath Lake basin experienced sustained loss of equilibrium at pH 10.75, 10.73, and 9.55, respectively. Saiki et al. (1999) calculated a mean 96-hr LC_{50} value of 10.30 for Lost River and 10.39 for shortnose suckers (3-7 month old juveniles). During the fish kills, pH was at some of the lowest values of the season, as would be expected during periods of algal biomass decline (Kann 1999), and was always less than 9.0 during the peak (Fig. 5).

Ammonia

Prior to the fish kills, un-ionized ammonia was frequently at levels that can damage gills, reduce oxygen carrying capacity of blood due to acidemia (Sousa & Meade 1977, and references therein), and damage the liver and kidney (e.g., Smith & Piper 1975; Wajsbrot et al. 1993). In their review of water quality standards, Alabaster and Lloyd (1980) reported that the acute lethal concentration of un-ionized ammonia ranged from 200 to 2000 $\mu g\ L^{-1}$ NH_3 for a variety of fish species, and that short-term exposure to lower concentrations may exert adverse physiological or histopathological effects. The mean 96-hr LC_{50} of un-ionized ammonia was 780 $\mu g\ L^{-1}$ for 100-day old shortnose suckers and 530 $\mu g\ L^{-1}$ for Lost River suckers (Saiki et al. 1999). In Upper

Klamath Lake, summer un-ionized ammonia commonly exceeded 200 µg L^{-1}, and reached 2000 µg L^{-1} at Shoalwater Bay in 1997 (Fig. 7); but, un-ionized ammonia was less than 200 µg L^{-1} during the fish kills (Figs. 5 and 7). The decline in NH_3 that occurred before each of the fish kills coincided with reduced algal biomass and reduced pH (pH affects the proportion of total ammonia that is un-ionized).

Dissolved Oxygen

The peak of the fish kills was consistently associated with low DO and sharply decreased algal abundance (Figs. 5 and 8), the latter contributing to low DO via reduced photosynthesis and increased biological oxygen demand (Barica 1974 and 1978; Wedemeyer et al. 1976). Dissolved oxygen levels associated with fish kills were typically less than 4 mg L^{-1} for 10-24 hours per day (at 1 m depth), for several days (Fig. 8). In most instances, these included shorter periods with DO 0-2 mg L^{-1}. These levels are well within the range shown to have lethal and sublethal effects on fish. The mean 96-hr LC_{50} values for DO were 1.6 mgL^{-1} for Lost River sucker juveniles and 1.3 mg L^{-1}, for shortnose sucker juveniles (Saiki et al. 1999). Sublethal effects associated with low DO include reduced growth, fecundity, and swimming ability (e.g. Doudoroff & Shumway 1970; Alabaster & Lloyd 1980; Barton & Taylor 1996). In Upper Klamath Lake, benthic fish such as suckers may suffer greater sublethal effects than our DO measurements at 1 m depth would indicate because of exposure to low off-bottom DO levels (e.g., while foraging) during times when DO levels were adequate elsewhere in the water column.

Fish mortality after the collapse of *A. flos-aquae* blooms is a common characteristic of many shallow lakes (e.g., Mackenthun et al. 1948; Ayles et al. 1976). Barica (1974) noted that anoxic conditions from *Aphanizomenon* collapse prevailed in the whole water column and typically lasted several days. Mericas and Malone (1984) also noted that "…oxygen depletion associated with fish kills was not a strictly diurnal phenomenon, but typically last for several days". These observations are similar to those from the fish kills in Upper Klamath Lake, except that hypoxic conditions in Upper Klamath Lake sometimes occurred over a longer period of time due to variation in the timing of algal collapse at different sites (e.g., 1997; Fig. 8.

Supersaturated levels of DO occurred frequently in Upper Klamath Lake. Fish kills from gas supersaturation are typically associated with dam spillways, but instances of fish kills from photosynthetically-elevated DO have been reported (Woodbury 1942). Incidences of supersaturated DO were not prevalent during the fish kills, and signs of gas bubble disease such as gas emboli under the skin were not observed in dead fish.

Algal Toxins

Two algae species (*A. flos-aquae* and *Microcystis aeruginosa*) in Upper Klamath Lake have been documented to produce toxins lethal to fish (Gentile & Maloney 1969; Carmichael 1986). However, *A. flos-aquae* from Upper Klamath Lake have shown no neurotoxin production (Carmichael et al. 2000). *Microcystis aeruginosa* from Upper Klamath Lake (an occasional co-bloomer with *A. flos-aquae*) produce the potent liver toxin microcystin (W. Carmichael, Department of Biological Sciences, Wright State University, personal communication) and assays of a few fish from the 1996 die-off indicated exposure to microcystin, but the extent of exposure could not be determined (B. Kotak, Algal Tox International**,** personal communication). However, none of the recent fish kills appeared biased toward smaller fish, as might be expected if toxins had contributed significantly to the die-offs (Wedemeyer et al. 1976; Meyer & Herman 1990); rather, the fish kills in 1995 and 1996 exhibited the opposite size selectivity.

Disease

Columnaris disease has received consideration as the mechanism causing death in Upper Klamath Lake fish kills because it was prevalent among several dozen dead suckers collected in 1995-97 (S. Foote, U.S. Fish and Wildlife Service; R. Holt, Oregon Department of Fish and Wildlife, personal communications). Columnaris is a bacterial disease caused by *Flavobacterium columnare,* which is common in aquatic ecosystems and often occurs in healthy fish (Austin and Austin 1987). *Flavobacterium columnare* is usually not pathogenic at temperatures less than 15^{o}C unless virulent strains are involved (Wakabayashi 1991; Noga 1996). As temperature increases, the acuteness of columnaris disease and the resultant mortality also increase (e.g., Pacha & Ordal 1970; Wakabayashi & Egusa 1972; Becker & Fujihara 1978). The fish kills in Upper Klamath Lake occurred during periods of declining temperature, 18-46 days after the peak daily mean water temperature (Fig. 5), which contradicts expectations had columnaris been the primary cause of the fish kills. The size selectivity of the fish kills and the movement of fish into spring areas and out of the lake (Williamson River and the A Canal) at the time of the fish kills (see below) are also not readily congruent with columnaris as the primary cause of the kills.

Conclusions

Based on the biological and water quality data, we concluded that hypoxia, caused by the collapse of *A. flos-aquae* blooms, was the primary mechanism that triggered the 1995-1997 fish kills. The susceptibility of fish to hypoxia was probably enhanced by chronic exposure to stressful levels of pH, ammonia, and DO during summer months prior to and during initiation of the kills. Wedemeyer et al. (1984) noted that stressful levels of one variable may lower tolerance to another. For example, low dissolved oxygen increases the toxicity of ammonia to fish (Lloyd 1961). Similarly, Bowser et al. (1983) found that an oxygen concentration of 4-5 mg L^{-1}, which would normally be adequate for channel catfish (*I. punctatus*), was not sufficient when simultaneously exposed to nitrite. In some instances, the effects of multiple stressors may be synergistic, rather than additive (Magaud et al. 1997). Differences in the fish composition of the 1995-97 kills were attributed to differences in the severity of the stressors. For example, in the year when DO and ammonia were most stressful (1997), the fish composition was the least species and size selective.

Substantial mortality occurred in Upper Klamath Lake after hypoxic conditions had apparently abated (Fig. 8). This may be explained partly by temporal and spatial variability in hypoxia that was not encompassed by data collection sites; however, disease probably caused considerable post-hypoxic mortality. Stressful water quality conditions such as low DO and high ammonia are known to increase the probability of disease (Burrows 1974; Smart 1976; Snieszko 1974; Chen et al. 1982). Moreover, disease outbreaks typically do not occur unless stressful environmental conditions have compromised the host defense system and predisposed fish to infection (Wedemeyer & McLeay 1981; Herman 1990). We concur with Herman (1990) that in such instances, although bacteria may be the clinical cause of death, the stressors (in this case poor water quality) should be considered the primary cause of death. Hence, the observation of columnaris among some fish from the kills in Upper Klamath Lake probably represented a secondary effect.

Considerable evidence indicates that phytoplankton community of Upper Klamath Lake historically had a mixed-species community, rather than the near-monoculture blooms of *A. flos-aquae* that have dominated in summer and fall for the past 50 years. Reports indicate that *A. flos-aquae* was scarce in the early 1900s (Kemmerer et al. 1923), abundant but not dominant in the late 1930s (Bonnell & Mote 1942), and dominant in a mixed algal community in the late 1950s (Phinney & Peek 1961). Analysis of resting spores produced by *A. flos-aquae* (akinetes) from sediment cores indicates a similar progression in the abundance of *A. flos-aquae*, and a reverse pattern for the green algae *Pediastrum* spp. (P. Bradbury and S. Coleman, U.S. Geological Survey, Woods Hole, personal communication). The shift in the phytoplankton community to *A. flos-aquae* is a fundamental alteration of the lake's ecosystem, which may have resulted from other ecosystem changes such as an altered hydrologic regime; loss of riparian, wetland, and lacustrine habitat; and increased nutrient input (Snyder & Morace 1997; Kann & Walker 1999). One outcome of this phytoplankton shift has likely been an increased frequency of poor water quality and fish kills.

The 1995-1997 fish kills provide a graphic indication of poor water quality, but should not be used as the only indicator. Poor water quality may occur without a large adult fish kill simply because of low fish abundance (e.g. 1992 and 1994; Fig. 6). In Upper Klamath Lake, few adult suckers existed from at least the early 1980s until 1995; hence, the probability of suckers occurring in a die-off were low, regardless of water quality. Poor water quality also causes sublethal effects such as reduced usable habitat, as observed in Upper Klamath Lake (M. Buettner, Bureau of Reclamation, personal communication), and physiological stress responses (e.g., Barton and Taylor 1996) that require energy expenditure and presumably contribute to observations of decreased growth, decreased swimming capacity, and increased probability of disease which have been associated with low DO (Doudoroff and Shumway 1970; Snieszko 1974).

The negative effects of poor water quality on the endangered suckers in Upper Klamath Lake have been substantial, both through lethal and sublethal effects. Stock assessments indicated that between 1995 and 1998, the abundance of spawners decreased 84% for Lost River suckers and 95% for shortnose suckers (Perkins et al. 2000). The extent of these decreases is probably underestimated because in the absence of the fish kills, abundance would have been expected to increase due to recruitment. Most of this decrease was clearly due to mortality from the fish kills, but some of the decrease may also have been due to sublethal effects such as poor physical condition and non-maturation of some adults. Suckers collected during the fish kills, as well as those captured in assessments the following spring, had a high incidence of afflictions such as parasitic and bacterial infections, cysts, and ulcers. These signs of stress suggest that poor water quality is probably having sublethal effects that reduce fitness.

Poor water quality caused by the predominance of *A. flos-aquae* is a major factor responsible for the decline of Lost River and shortnose suckers. The fish kills studied were preceded by, and in some cases initiated during, a period of high pH, high un-ionized ammonia, and low off-bottom dissolved oxygen. This was followed by several days of low dissolved oxygen that extended throughout the water column. Elevated pH, low dissolved oxygen, and high un-ionized ammonia are directly related to *A. flos-aquae* blooms, and are components of water quality linked to fish health, fitness, and survival in Upper Klamath Lake. Thus, the predominance of *A. flos-aquae* has contributed to the decline of these endangered suckers. These species exhibit life history strategies similar to the "periodic strategist" described by Winemiller and Rose (1992), which is characterized by strong year classes that occur periodically. This life history strategy relies upon low adult mortality and longevity to persist through extended periods of poor recruitment. Recurrent events, such as fish kills, that increase adult mortality disrupt this life history strategy and may jeopardize long-term population viability.

Restoration of better water quality to Upper Klamath Lake is critical for the recovery and conservation of the endangered suckers because the lake represents the majority of remaining habitat for both species. Long-term restoration efforts should focus on shifting the phytoplankton community toward a mixed-species assemblage as once existed, which would be less likely to develop extreme biomass levels and cause die-offs (Barica 1978). Lost River and shortnose suckers are highly fecund species that have the capacity to rebound rapidly from population declines, but only if suitable environmental conditions exist.

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